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48

49 **Running headline:** LDMC and SLA as predictors of primary production.

Summary

1. Reliable modelling of above-ground Net Primary Production (aNPP) at fine resolution is a significant challenge. A promising avenue for improving process models is to include response and effect trait relationships. However, uncertainties remain over which leaf traits are correlated most strongly with aNPP.
2. We compared abundance-weighted values of two of the most widely used traits from the Leaf Economics Spectrum (Specific Leaf Area and Leaf Dry Matter Content) with measured aNPP across a temperate ecosystem gradient.
3. We found that Leaf Dry Matter Content (LDMC) as opposed to Specific Leaf Area (SLA) was the superior predictor of aNPP (R^2=0.55).
4. Directly measured *in situ* trait values for the dominant species improved estimation of aNPP significantly. Introducing intra-specific trait variation by including the effect of replicated trait values from published databases did not improve the estimation of aNPP.
5. Our results support the prospect of greater scientific understanding for less cost because LDMC is much easier to measure than SLA.

Key-words: Bayesian modelling, ecosystem, global change, measurement error, ecosystem function, intra-specific variation,

Introduction

Net Primary Production (NPP), defined as the rate at which plants convert CO_2 and water into dry matter, is the basis for life on Earth and is a fundamental ecosystem function supporting food production, soil formation and climate stabilisation. An estimated 28.8% of global NPP (Haberl *et al.* 2007) is appropriated by humans as food, fibre and fuel with consumption often spatially far removed from the area of production (Erb *et al.* 2009).

77 Accurate prediction of NPP is therefore critical to ecological and economic assessments of
78 the links between land-use change, human well-being and impacts on biodiversity and other
79 ecosystem services (DeFries 2002; Haberl *et al.* 2007). NPP is, however, challenging to
80 measure and predict accurately (Cramer *et al.* 1999; Scurlock *et al.* 2002; Jung *et al.* 2007). A
81 way forward is to derive regionally applicable relationships between plant traits and NPP
82 thereby providing empirical understanding that can potentially be built into global
83 ecosystem models to improve their performance (Wright *et al.* 2006; Van Bodegom *et al.*
84 2012). New empirical predictions of NPP in terms of plant trait abundance also allow
85 process models to be tested at fine resolution across a range of ecosystems.

86 Trait-based ecology has become a unifying strand in global change biology because the
87 same sets of key plant traits respond to global change drivers while also driving subsequent
88 effects on ecosystem function (Tateno & Chapin 1997; Suding *et al.* 2008; Reich 2014). We
89 test the performance of two leaf traits – Leaf Dry Matter Content (LDMC) and Specific Leaf
90 Area (SLA) – as predictors of above-ground NPP (aNPP) across a realistically wide
91 productivity gradient using comprehensive measurements of aNPP comprising the full range
92 of plant functional types that dominate temperate ecosystems. Our study seeks to resolve
93 an outstanding question concerning the relative merits of each trait as a correlate of soil
94 fertility and ecosystem productivity (Wilson *et al.* 1999; Hodgson *et al.* 2011). LDMC and SLA
95 both correlate strongly with nutrient availability but it is not clear which of these is the best
96 predictor of aNPP (Wilson *et al.* 1999; Ordoñez *et al.* 2009; 2010; Fortunel *et al.* 2009;
97 Hodgson *et al.* 2011; Pakeman 2011). Given its repeatedly proven alignment with the soil
98 available nutrients axis, SLA has become the pre-eminent predictive leaf trait (Reich 2014).
99 However, the sensitivity of SLA to light availability means that it is not a reliable partial

predictor of soil fertility as irradiance changes during succession. Since primary production reflects the availability of resources that include light and nutrients it could mean that SLA is actually a better predictor of aNPP. To test this relationship requires treating SLA as an effect trait rather than as a response trait where variation in abundance-weighted values are explained by abiotic factors (Hodgson *et al.* 2011).

Unlike SLA, LDMC varies independently of leaf thickness (Shipley 1995; Wilson *et al.* 1999; Roche *et al.* 2004) but is also strongly correlated with resource availability and with relative growth rate (Weiher *et al.* 1999; Garnier *et al.* 2004; Fortunel *et al.* 2009). LDMC has been recommended as a more reliable correlate of soil fertility at least in biomes not subject to severe water limitation (Vendramini *et al.* 2002). Here we explore the role of SLA and LDMC as predictors of ecosystem function and ask which best predicts aNPP across ecosystems. Since there has been a growing appreciation of the influence of within-species trait variation (Albert *et al.* 2010; Siefert *et al.* 2015) we also test whether including intra-specific trait variation improves the fitted relationship between traits and aNPP. We investigate the performance of each trait as a predictor of aNPP when species of low abundance are excluded and when plant species abundance-weighted trait values for the dominant species among habitats are based on database values or *in situ* measurements.

Our starting point was to compute abundance-weighted trait values based on published UK database values. This is the easiest method to apply for constructing trait-derived variables. However, if locally measured trait-values differ appreciably from database means and correlate with aNPP then database-derived means will be a poorer predictor of local aNPP. We tested the importance of intra-specific variation in two ways. First, we substituted mean

123 database trait values for the dominant species in each sampling plot with *in situ*
124 measurements of leaf traits for those species. The two most abundant species were
125 selected to ensure adequate sampling of the species contributing the most biomass to each
126 stand. Secondly, we introduced intra-specific trait variation via its effect on the variance of
127 the abundance-weighted mean trait values. Thus, rather than employing one abundance-
128 weighted mean trait value per sampling plot, a prior distribution of values was calculated
129 based on repeated draws of trait values for each individual plant species. The distributions
130 of trait values for each species were derived from readily accessible replicated database
131 measurements. We then applied a Bayesian measurement error model that allows the
132 observed values of aNPP to feedback onto the posterior estimates of the abundance-
133 weighted trait values potentially improving the fit between aNPP and trait-based
134 explanatory variable. If successful, this would suggest that better use could be made of the
135 variation in trait values that is readily accessible from databases, rather than just utilising
136 trait means.

137

138 In summary we test the following hypotheses:

139 1. Abundance-weighted LDMC is a better predictor of aNPP than abundance-weighted
140 SLA.
141 2. Estimation of aNPP is improved when trait values for the dominant plant species are
142 based on *in situ* measurements rather than database averages.
143 3. Estimation of aNPP is improved when intra-specific trait variation based on
144 replicated database values is included in the model.

145

Materials and Methods

Study region and sampling locations

Fifteen sites were located in the River Conwy catchment in north Wales, UK. The remaining two sites (limestone grassland and upland unimproved hay meadow) were located within the Ingleborough National Nature Reserve in North West England in the upper reaches of the Ribble catchment (Fig. 1; Table 1). The regional climate for all sites is temperate maritime (Peel, Finlayson & McMahon 2007). Annual precipitation lies between 1000 and 1300 mm at Ingleborough and between 600 and 4700 mm in the Conwy valley. Average daily minimum January temperature across the sites is in the range -1 to 3 °C and average daily maximum July temperatures from 17 to 21 °C (long term annual averages 1981-2010, http://www.metoffice.gov.uk/public/weather/climate/#?region=uk).

Above-ground NPP was measured in 49 vegetation sampling plots through 2013 and 2014. These plots were nested into 17 sites arranged along a productivity gradient from lowland grasslands intensively managed for agriculture through to montane heath. Within each site, an area of target habitat was selected as a roughly rectangular fraction of the wider habitat of interest. In enclosed land this rectangle was defined by field boundaries. In woodlands and unenclosed habitats a rectangular area was selected to encompass a large area (0.25-1 ha) of the target habitat, for example blanket bog, acid grassland and montane heath. Sampling locations within each site were then chosen at random. Together, these sites sample all common habitat and land-use types in Britain and thus were intended to represent the principal plant biodiversity and productivity gradients in NW Europe.

Measurement of above-ground Net Primary Production

Above-ground NPP (g dry mass m^{-2} yr^{-1}) was measured using a variety of methods according to the plant functional types present. These types comprised C3 graminoids (Poaceae, Junaceaa, Cyperaceae), broad-leaved and needle-leaved trees, dwarf shrubs, forbs and bryophytes (Table 1). All plots were visited in early January at the start of each measurement year. Any green herbaceous material was removed by clipping to 1 cm vegetation height. Standing litter was, as far as possible, not removed nor disturbed. In sheep and cattle-grazed systems (grasslands and mires), livestock exclosures were installed and the vegetation cut twice throughout the growing season; first at estimated peak biomass and a second time to capture late summer and autumn regrowth. These two values were then summed. While this method does not overcome possible issues with negative and positive compensatory growth as a result of grazing, uncertainty over the importance and direction of these effects is great and no clearly superior method appears to exist that accounts for these effects whilst also excluding grazers (McNaughton *et al.* 1996; Pontes *et al.* 2007).

The biomass fractions attributable to functional types within woodland and peatland ecosystems were measured using differing methods. In peatlands, growth of *Sphagnum* species was measured over two years using the cranked wire method (Clymo 1970; Kivimäki 2011). Peatland graminoids were measured by harvesting annual biomass accumulation in livestock exclosures over one year using the same methods applied to grazed grasslands.

In woodlands, different methods were used to measure annual production of trees. Leaf litter was collected using 20 randomly placed buckets (26cm in diameter) per 200m^2

196 sampling plot. These were installed in September before litterfall and visited and emptied
197 every two to four weeks until no leaves were visible in the canopy. Annual woody mass
198 increment was measured by combining tree-coring, DBH (tree diameter at 1.3 m height),
199 wood density and tree height measurements. Herbaceous understorey growth was
200 harvested in spring and summer after cutting back in January. Where present, annual
201 production of the bryophyte layer was measured by harvesting the moss mat that had
202 grown through coarse plastic meshes of known size pegged securely to the substrate in
203 early January and harvested after one year.
204
205 Measurement of aNPP was carried out using plots of varying dimensions scaled to the size
206 of the plant types present, but then expressed as production per m^2 across all vegetation
207 types (Table 1). Full details of all the methods used for measurement of aNPP on each site
208 are described in Supplementary Material.
209
210 Plant species abundance
211
212 In each plot in which aNPP was measured, all vascular plant species and bryophytes were
213 identified and cover was estimated in intervals of 5 % except for species recorded at ≤1 %
214 cover which were given a value of 1. Percentage cover was based on horizontal leaf
215 projection over the plot so that total cover over all species was allowed to exceed 100, for
216 example, where the understorey comprised a bryophyte layer, a fern layer and a tree
217 canopy. Only species recorded with ≥5 % cover were used in the calculation of mean
218 abundance-weighted trait values.

219

220 Plant traits

221

222 *In situ* measurements of SLA and LDMC were carried out by focussing on the dominant
223 vascular plant species in each plot defined as the two species contributing maximum
224 standing biomass in the year of sampling (Table 1). LDMC (g dry mass g^{-1} fresh mass) was
225 measured by weighing fresh material consisting of 10 to several hundred mature but non-
226 senescent leaves from different plants depending on leaf size. Leaves were weighed fresh,
227 then dried for 24 hours at 80 ^{o}C, and weighed again. SLA (mm^2 mg^{-1} dry mass) was measured
228 by sampling 10 leaves from different plants. Leaf area was calculated based on scanned
229 photographs analysed using the Image J software v1.46r (http://imagej.nih.gov/). Dry
230 weight was measured as for LDMC (Pérez-Harguindeguy *et al.* 2013).

231

232 Database values for SLA and LDMC for all vascular plant species encountered in the sample
233 were extracted from LEDA (Kleyer *et al.* 2008) and ECPE (Grime *et al.* 2007). Only values for
234 UK material were included except in four instances where German values were included
235 because no UK data were available. These were *Carex bigelowii*, *C.nigra*, *Agrostis canina* and
236 *Anthoxanthum odoratum*. None of these species were dominant in any of the sample plots.
237 Out of a total pool of 136 vascular plant species recorded in the 49 aNPP plots all had
238 database trait values. The ranges of trait values, including measured and database values,
239 were 57.2 for SLA (4.81, *Picea sitchensis* to 62.1, *Oxalis acetosella*) and 0.45 for LDMC (0.08,
240 *Stellaria media* to 0.53, *Sesleria caerulea*).

241

242

243 Analysis

244

245 Mean abundance-weighted trait values (x_{jk}) for SLA and LDMC were computed for each

246 NPP sampling plot *j* within each site *k* as follows;

247

248

249

250 $$x_{jk} = \sum_{i} \frac{\tau_{ijk} p_{ijk}}{\sum_i p_{ijk}}$$

251

252

253 where (p_{ijk}) was either the raw percentage cover or square-root transformed cover value for

254 species *i* in each sample plot *j* within site *k* (e.g. Manning *et al.* 2015). The trait values (τ_{ijk})

255 for each species *i* in each sample plot *j* and within site *k* were based either on replicated *in*

256 *situ* measurements on the two plant species with the highest cover in each plot, or mean

257 values of each trait extracted from the databases described above.

258

259 Two values of the mean abundance-weighted trait (SLA or LDMC) were derived for each plot

260 based on either trait values derived solely from UK databases or supplemented by *in situ*

261 trait measurements for the dominant species in each plot where this value substituted for

262 the database average for those species (Table 1). Abundance-weighted values for SLA and

263 LDMC were used as covariates in regression models designed to test the three hypotheses

264 by determining which model best predicted measured aNPP.

265

266 Statistical modelling

267

268 Model building was carried out using the 'lm' and 'lmer' functions in the lme4 R package

269 (Bates *et al.* 2015). Initial data exploration and preparation followed the steps outlined in

270 Zuur *et al.* (2010) and Crawley (2013). We identified outliers using the outlierTest function in

271 the 'lm' R package. The boxcox function in the 'mass' R package was used to assess

272 homogeneity of variance and the nature of any transformation required to aNPP.

273

274 Tests of hypotheses 1 to 3 were carried out by comparing models where each model was of

275 the form,

276

277 $y_{ik} = m_{ik} + \gamma_k + \varepsilon_{ik}$, 1)

278

279 $m_{jk} = a + b.x_{ik}$ 2)

280

281 $\gamma_k \sim N(0, \sigma_\gamma^2)$

282

283 $\varepsilon_{ik} \sim N(0, \sigma_\varepsilon^2)$.

284

285 Where y_{jk} was the natural log transformed aNPP for plot *j* in site *k*, x_{jk} was the abundance-

286 weighted trait variable and γ_k was a random intercept for each site *k*.

287

Model performance was evaluated by likelihood ratio test and the difference in AICc values between pairs of models. The AICc statistic was used in light of the small sample size (Burnham & Anderson 2002).

To test whether estimation of aNPP was improved by the inclusion of intra-specific trait-variation (Hypothesis 3), a Bayesian measurement-error model was constructed in OpenBUGS ver 3.2.2 rev 1063 (Lunn *et al.* 2013). We modelled the variation in abundance-weighted trait values in each plot by adjusting equation 2) to become,

$$m_{jk} = a + b.z_{jk} \quad 3)$$

$$x_{jk} \sim N(z_{jk}, \sigma_x^2).$$

Here, we now assume that the observed abundance-weighted mean x_{jk} is an imperfect measure of the true abundance-weighted mean z_{jk} with its variance being a function of the distributions of species' trait values contributing to the abundance-weighted trait value for each aNPP plot. These distributions were derived from published replicated database measurements of the trait for each species present. The variance of each species trait value is, therefore, likely to be part measurement error and part ecologically meaningful intra-specific variation in the trait. Thus, σ_x^2 conveys the variance in the trait-derived predictor of aNPP that is attributable to known variation in the trait for each contributing species in each plot. An estimate of σ_x^2 was generated by first calculating the mean and standard deviation of the database measurements for each plant species which had replicate measurements in

311 the database. Then 1000 random draws of trait values were made based on the parameters
312 of each species' trait distribution. At each draw, a new dataset of abundance-weighted trait
313 values was computed for each of the aNPP plots. An estimate of σ_x^2 was then derived by
314 drawing bootstrap samples of increasing size from this dataset until its value stabilised (Fig.
315 S1). Note that this approach implicitly assumes that measurement errors are independent
316 between species and plots. Since we did not derive the trait distributions from measured
317 values from all the species populations within each plot, we cannot directly test this.
318
319 The fitted Bayesian measurement error model allows feedback from the aNPP data such
320 that model fit can potentially be improved. Thus the posterior distribution of the slope *b*
321 (Equation 3) is also a function of new updated posterior distributions for the abundance-
322 weighted means that optimise the fit between these and aNPP. Without feedback, the
323 effect of intra-specific variation on the abundance-weighted trait means would simply
324 increase the uncertainty around the estimated slope. Measurement error models with
325 feedback are common in pharmacokinetic studies (see Lunn *et al* (2009; 2013) for further
326 details and discussion).
327
328 Hypothesis 3 was tested by comparing models with or without intra-specific variation
329 (Equations 2 versus 3). We computed the marginal R^2 (m) value of Nakagawa & Schielzeth
330 (2014) for each model within our BUGS code. This quantifies the explanatory power of the
331 fixed effects (abundance-weighted trait values) as a proportion of the sum of all the
332 variance components; fixed effects plus random effects plus residual. Tests of the difference
333 in R^2 (m) between models were carried out by inspecting the 95 % credible interval (2.5 %

and 97.5 % quantiles) of the distribution of differences between 1000 values of R^2 (m) drawn randomly from the posterior distribution of the variable for each model to see whether or not it contained zero. This was achieved in an R script applied to the converged MCMC output for R^2 (m).

The percentage variance attributable to the random effect of site was also calculated with and without the fixed trait effect. This firstly conveys the amount of variation in aNPP between versus within sites and then estimates the extent to which these differing components of variation in aNPP were explained by the abundance-weighted trait (Crawley 2013).

Results

Initial data exploration showed that aNPP should be transformed to achieve normally distributed residuals and a linear response to abundance-weighted traits. The boxcox function (R package MASS) was applied, confirming that a natural log transformation was most appropriate. Models were also fitted with either untransformed, or square-root transformed plant species cover values in an attempt to reduce the influence of recording error associated with small differences in % cover. Seven out of eight models based on square-root transformed cover had lower AICc values than the respective model with untransformed cover. In three cases, including the final best fitting model, the difference was greater than the rule-of-thumb value of 2 (Table S2). Thus all subsequent modelling was performed using abundance-weighted trait variables calculated from square-root transformed cover.

Across the 49 plots nested into 17 sites, measured aNPP ranged from 99 g dry mass m^{-2} yr^{-1} in montane heath to a maximum of 1481 g dry mass m^{-2} yr^{-1} in intensively-managed lowland improved grassland (Fig. 2). Overall, 91 % of the variation in aNPP occurred between sites. AICc values for models based on abundance-weighted LDMC were all lower than for models including only SLA (LDMC: 25.6 for a model based on *in situ* trait measurements for the dominants and 30.7 for a model derived from database values only. SLA: 44.8 for a model based on *in situ* trait measurements for the dominants and 42.1 for a model derived from database values only) and differed significantly from these models based on likelihood ratio tests. Thus LDMC was the better trait for predicting aNPP and the best model included *in situ* measurement of LDMC on the dominant species. Hypotheses 1 and 2 were, therefore, supported.

When intra-specific variation in LDMC was included, the model with the highest R^2 (m) included *in situ* trait measurements and the effect of variation in LDMC derived from replicate values in the database. This model explained 55% of the variation in ln(aNPP) with a 95% credible interval of 0.34-0.71, but its R^2 (m) value was not significantly different from a model without database-derived intra-specific variation when their differences were bootstrapped. The model with the highest R^2 (m) explained 63 % of the within-site, between-plot variation and 34 % of the between-site variation.

Discussion

LDMC versus SLA?

We show that LDMC is a superior predictor of aNPP compared to SLA. Our result is novel since we tested SLA and LDMC as *effect* traits across a gradient comprising all major terrestrial ecosystems in the temperate zone. This contrasts with the large number of studies that have explored their role as *response* traits expressing inter- and intra-specific trait variation as a function of environmental gradients such as climate and soil conditions. While LDMC was the superior trait, low variance was explained. In particular, abundance-weighted LDMC only explained a relatively small proportion of the between-site variance that dominated the dataset. It is possible that other plant species-derived predictors could be usefully included in the analysis to increase explanatory power. Leaf traits exhibit differences between plant functional types that are linked to phylogenetically-conserved patterns of biomass allocation (Shipley 1995; Wilson *et al.* 1999; Wright *et al.* 2005; Poorter *et al.* 2012). Therefore, introducing proportional cover of each plant functional type might be worthwhile. However, such categorical units have reduced information content because they do not express continuous variation in plant properties that influence ecosystem function (Van Bodegom *et al.* 2012). This is especially critical for our study. Because we included a range of successional stages across sites and because our sites were located in the oceanic western edge of Europe, the most obvious additional axes of functional variation across our dataset are plant height and bryophyte cover. In forest ecosystems, aNPP may poorly correlate with lower SLA or higher LDMC because lower production per mass of leaf is compensated by higher absolute foliage mass (Wright *et al.,* 2005; Garnier *et al.,* 2004). When we included abundance-weighted canopy height alongside abundance-

403 weighted LDMC, it failed to explain significant variation in aNPP (see Supplementary
404 Material; Text S1, Table S1, Fig. S3). Because a number of bryophyte genera, including
405 *Sphagnum*, are capable of fixing atmospheric nitrogen (Cornelissen *et al.* 2007), the
406 inclusion of bryophyte cover was also tested as an additional predictor alongside LDMC and
407 SLA but this was also not significant (see Supplementary Material; Text S1, Table S1, Fig. S3).
408 It is quite possible that the addition of climate variables could have explained further
409 variation in aNPP. We did not explore this because (a) we expect considerable collinearity
410 between climate and abundance-weighted trait means (e.g. Ordoñez et al 2009) and (b), our
411 principal aim was to explore the ability of each trait to explain variation in aNPP rather than
412 to develop a full, empirical predictive model for aNPP. While an advantage of our study is in
413 the breath of ecosystem variation sampled, this also trades-off against our ability to
414 measure and model ecosystem-specific factors and their interactions that are likely to have
415 more fully explained observed aNPP (e.g. Minden & Kleyer 2015).
416
417 There are a number of possible reasons why LDMC outperformed SLA in our analysis. SLA
418 exhibits a plastic response to irradiance via changes in leaf thickness such that values can
419 vary significantly with canopy depth even on the same tree (Hollinger 1989). Thus thin
420 shaded leaves have high SLA because they optimise light capture rather than being
421 associated with high soil fertility and therefore higher aNPP (Hodgson *et al.* 2011). These
422 erroneous SLA signals may well have contributed to the variation in published database
423 values and so to poorer performance of SLA in our analysis of database-derived means.
424 However, if intra-specific trait variation is partly an adaptive response to local conditions,
425 then one might have expected LDMC to perform less well because it appears to be

426 somewhat less plastic than SLA across environmental gradients (Siefert *et al.* 2014; but see
427 Roche *et al.* 2004). Our result is consistent with other evidence. In a study investigating the
428 response of leaf plant traits to cutting frequency and nitrogen supply among temperate
429 grass species, many of which also dominated our grassland samples, Pontes *et al.* (2007)
430 found that within-species, between treatment-variation in SLA and LDMC was around 14 %
431 and that LDMC but not SLA was correlated with aNPP. Even where significant intra-specific
432 variation has been observed, it has proved difficult to explain by abiotic factors (Ordoñez *et*
433 *al.* 2009; Laughlin *et al.* 2012) often ending up as residual variance rather than predicting
434 local coupling between trait values and environmental (Albert *et al.* 2010; Jung *et al.* 2010).
435 This suggests that we might not expect a major jump in predictive power by including intra-
436 specific variation alongside inter-specific variation especially when derived from replicated
437 database measurements rather than *in situ* plant populations.
438
439 Field measurements versus database values
440
441 Our results indeed showed that including *in situ* field measurements increased explanatory
442 power to a greater extent than introducing intra-specific variation via replicated database
443 values. *In situ* measurements ought to be a better physiological reflection of the
444 performance of the particular vegetation stand than database averages, and this was indeed
445 found to be the case. It is likely that the residual error associated with our best model was in
446 part attributable to low *in situ* trait measurement effort. For example Baroloto *et al.* (2010)
447 recommended sampling each species at least once in every plot. Even this level of effort
448 may under-represent the variation that can occur in trait values between leaves on the

same plant (Shipley, 1995), between individuals of the same species (Albert *et al.* 2010) and throughout the growing season (Pierce *et al.* 1994; Gunn *et al.* 1999; Jagodziński et al 2016). Thus sampling a few individuals in a site at one point in time may lead to unrepresentative trait values poorly coupled to prevailing conditions. Evidently our level of *in situ* sampling effort was sufficient to improve model fit even though our best model still explained just over 55% of the variation in aNPP.

The extent to which *in situ* sampling should focus on capturing inter- or intra-specific variation depends upon the relative importance of each source of variation. Intra-specific variation appears to be greater in less species-rich ecosystems and towards the more extreme end of environmental gradients (Huslof *et al.* 2013; Siefert *et al.* 2015; Baroloto *et al.* 2010). In the absence of any *in situ* measurements, trait means must be calculated from existing databases. Cordlandwehr *et al.* (2013) showed that for less variable traits such as LDMC, database values could satisfactorily approximate ecosystem averages but would be less sensitive to between-patch variation within an ecosystem. Relying solely on database measurements may therefore only weakly capture trait-environment relationships (Manning *et al.* 2015). However, our results indicated that even when derived as database means, LDMC outperformed SLA in prediction of aNPP.

Conclusions

Using finely-resolved plant trait measurements across a representative vegetation productivity gradient, we show that LDMC was the superior predictor of aNPP compared to

SLA. Intra-specific variation, as expressed by *in situ* trait measurements of the two highest abundance species in each plot, led to improved estimation of aNPP but including trait variation as expressed in published database trait values did not. Thus, including database-derived intra-specific variation and allowing this to improve model fit is not an effective substitute for *in situ* trait measurements. However, since LDMC is much easier to measure than SLA, our results suggest that for prediction of aNPP, the burden of data collection can be reduced significantly, thereby offering the prospect of greater scientific understanding for less cost.

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Author contributions

SMS, MM, BE, LM, DJ, JC planned and designed the research. SMS, HG, MM, LM, SR conducted fieldwork and analysed data. SMS, ADB carried out the statistical modelling. All authors wrote the manuscript.

Data accessibility

Smart, S., Reinsch, S., Mercado, L., Blanes, M.C., Cosby, B.J., Glanville, H.C., Jones, D.L., Marshall, M.R. & Emmett, B.A. (2016). Plant structural measurements in North Wales and Northwest England 2013 and 2014. NERC Environmental Information Data Centre. https://doi.org/10.5285/8899768c-cc5a-4885-a88b-c08374ee568e.

Supplementary Material

Figure S1: Standard deviation of abundance-weighted LDMC values versus bootstrap sample size.

Fig S2: Exploratory plots of abundance-weighted traits against ln(aNPP).

Text S1: Additional modelling of bryophyte cover and canopy height.

Table S2: Comparison of models derived from either square-root transformed or untransformed cover data for each plant species in each sampling plot.

Text S2: Field methods for measuring above-ground Net Primary Production

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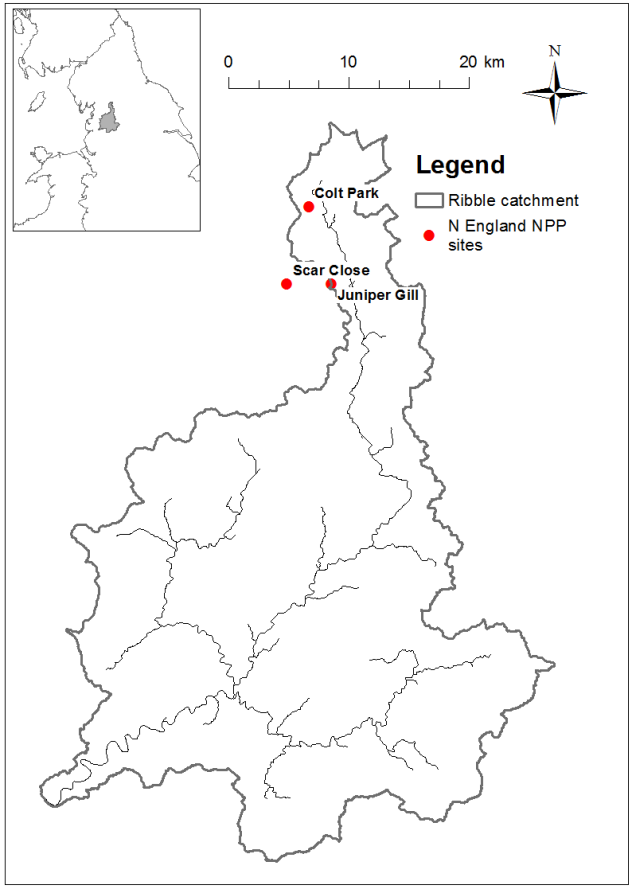
Figure 1: Maps showing the sample sites in (a) North West England and (b) North Wales.

a)



b)

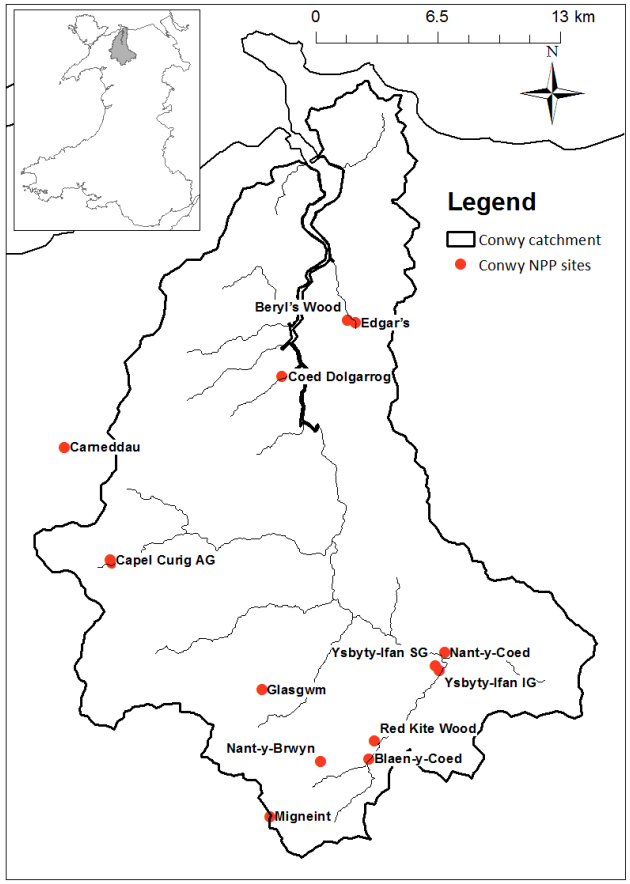


Figure 2: Measured above-ground NPP (aNPP) values across temperate ecosystem types sampled in 2013 and 2014. The median is shown as a black point. Boxes indicate the interquartile range and the whiskers the range of the measurements.

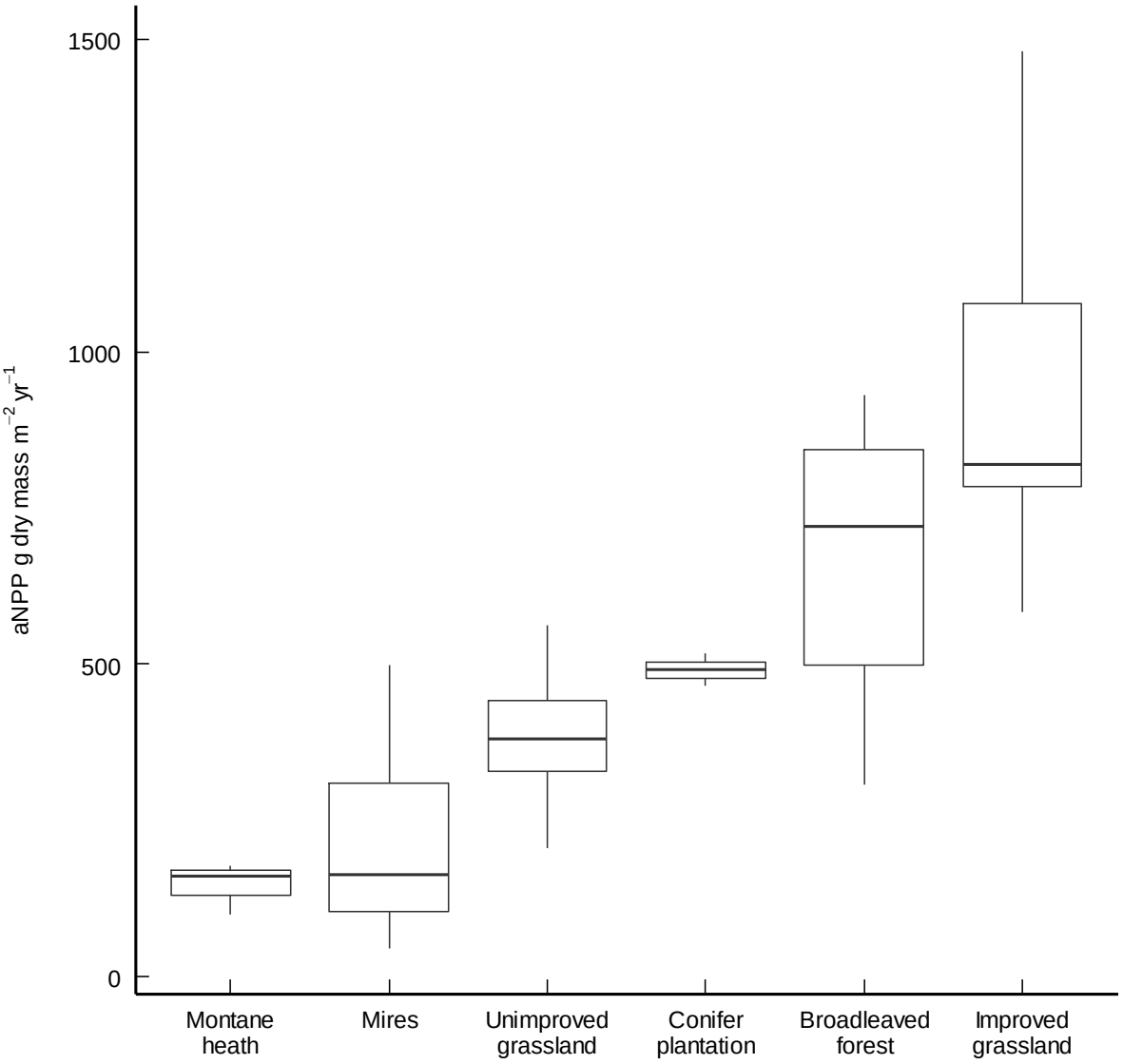


Figure 3: Best fitting model of ln(aNPP) predicted by cover-weighted Leaf Dry Matter Content incorporating the effect of database-derived intra-specific variation and including *in situ* trait measurements. R^2(m)=0.55. y=x line is shown.

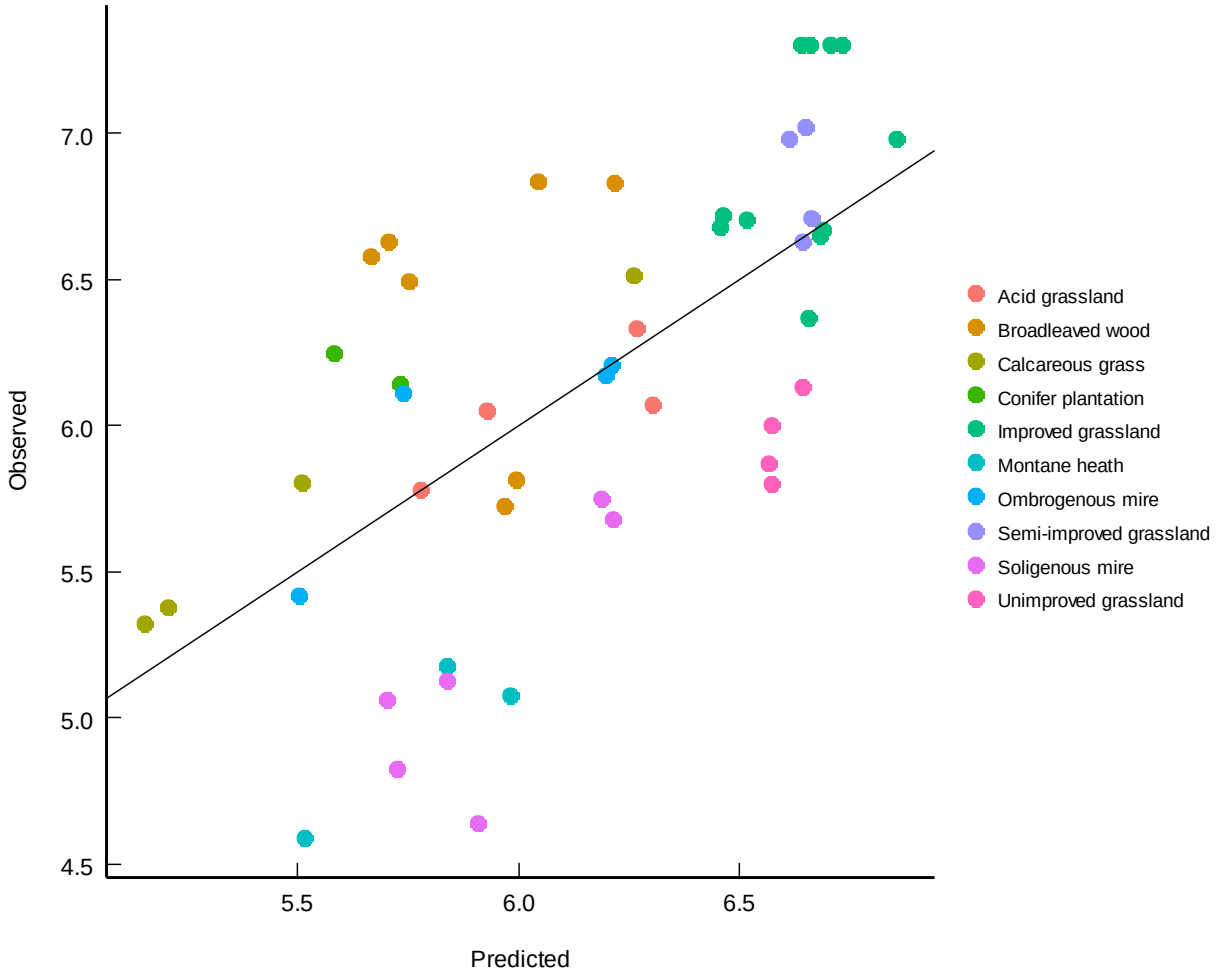


Table 1: Details of study sites and plots in which aNPP was measured. Sampling methods are fully described in Supplementary Material. Nomenclature for vascular plants follows Stace (1997) and Hill *et al.* (2008) for bryophytes.

Site	**Habitat type**	**Mean soil pH (0-15cm)**	**Management status**	**Dominant plant species**	**Number of plots (plot size)**	**aNPP methods**
Beryl's Wood	Broadleaved woodland	4.62	Unmanaged	*Quercus petraea/robur, Fraxinus excelsior, Betula pendula*	2 (200m^2 tree canopy), 3 (1m^2 understorey)	Understorey biomass harvest. Bryophyte mesh. Litter buckets. Annual woody increment from tree ring core, tree height & DBH.
Red Kite Wood	Broadleaved woodland	4.19	Unmanaged	*Acer pseudoplatanus*	1 (200m^2 tree canopy), 2 (1m^2 understorey)	As above.
Coed Dolgarrog	Broadleaved woodland	3.98	Unmanaged	*Quercus petraea/robur*	1 (200m^2 tree canopy), 2 (1m^2 understorey)	As above.
Glasgwm	Conifer plantation	4.2	30 year old Sitka subject to	*Picea sitchensis*	1 (200m^2 tree canopy), 2 (1m^2 understorey)	As above.

			past thinning			
Nant-y-Coed	Improved grassland	5.68	Highly intensive cattle grazing. Cattle rotated fortnightly across heavily fertilized paddocks.	*Lolium perenne*	4 (1m^2)	Two biomass harvests per year.
Blaen-y-Coed	Soligenous mire	4.56	Low intensity sheep grazing with periods unmanaged	*Molinia caerulea*	2 (1m^2)	As above.
Migneint	Ombrogenous mire	3.82	Last burnt 30+ years ago. Very light sheep grazing.	*Sphagnum capillifolium, Eriophorum vaginatum*	16 cranked wires among 4 patches of *Sphagnum*	Wire length measurements over two years.
Nant-y-Brwyn	Ombrogenous mire	4.26	Last burnt 30+ years ago. Very light sheep grazing.	*Sphagnum fallax, Juncus effusus*	4 (1m^2) 6 cranked wires among 3 patches of *Sphagnum*	Two biomass harvests per year. Wire length measurements over two years.

Llyn Serw	Ombrogenous mire	3.82	Last burnt 30+ years ago. Very light sheep grazing.	*Calluna vulgaris*	3 (1m^2 in each of 5, 11, 30 year old *Calluna*)	Total biomass harvest for growth curve construction.
Capel Curig VB	Soligenous mire	4.07	Very light sheep and cattle grazing.	*Molinia caerulea, Sphagnum papillosum*	4 (1m^2), 12 cranked wires among 4 patches	Two biomass harvests per year. Wire length measurements over two years.
Capel Curig AG	Acid grassland	4.81	Light sheep and cattle grazing.	*Deschampsia flexuosa, Nardus stricta*	4 (1m^2)	Two biomass harvests per year.
Carneddau	Montane heath	4.40	Light sheep grazing.	*Empetrum nigrum, Salix herbacea*	3 (0.25m^2)	One biomass harvest per year.
Juniper Gill	Calcareous grassland	7.46	Wild deer and rabbit grazed.	*Sesleria caerulea*	2 (0.25m^2)	Two biomass harvests per year.
Scar Close	Calcareous grassland	-	Wild deer and rabbit grazed.	*Sesleria caerulea, Pteridium aquilinum*	2 (0.25m^2)	Two biomass harvests per year.

Colt Park	Unimproved grassland	5.07	Traditional hay meadow; cattle and sheep in spring then shut up for summer hay growth, then aftermath grazed.	*Trifolium pratense, Anthoxanthum odoratum*	4 (0.25m^2)	Two biomass harvests per year.
Hiraethlyn	Improved grassland	4.59	Intensive sheep grazing.	*Lolium perenne, Holcus lanatus*	4 (1m^2)	Two biomass harvests per year.
Ysbyty-Ifan IG	Improved grassland	5.67	Intensive cattle and sheep grazing.	*Lolium perenne, Poa trivialis*	4 (1m^2)	Two biomass harvests per year.
Ysbyty-Ifan SG	Semi-improved grassland	5.58	Intensive cattle and sheep grazing.	*Lolium perenne, Holcus lanatus*	4 (1m^2)	Two biomass harvests per year.